Effects of seasonal grazing on forage production and quality within a long-term protected riparian zone

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"Effects of Seasonal Grazing on Forage
Production And Quality Within A Long-Term
Protected Riparian Zone"
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Effects of Seasonal Grazing on Forage Production and Quality Within a Long-Term Protected Riparian Zone

Final Report

for

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ABSTRACT

EFFECTS OF SEASONAL GRAZING ON FORAGE PRODUCTION AND QUALITY WITHIN A LONG-TERM PROTECTED RIPARIAN ZONE

Forage nitrogen (N) and phosphorous (P) concentrations and *in-vitro* dry-matter digestibility (IVDMD) were measured in 2 important riparian species the year following short-term, high intensity cattle grazing treatments in a montane riparian zone in north-central Colorado. In addition, peak standing crop of herbaceous vegetation was sampled on paddocks that were grazed the previous year.

Nitrogen, P, and IVDMD were the response variables used to determine effects of grazing and season of grazing in 1995 on forage quality the following growing season. Current year's growth of water sedge (*Carex aquatilus*) and planeleaf willow (*Salix planifolia*) were collected monthly from May through September, 1996. Nitrogen and phosphorous concentrations and IVDMD declined ($p<0.0001$) over the course of the growing season for both species. Nitrogen, P, and IVDMD in water sedge were different ($p<0.0001$) from those found for planeleaf willow. Planeleaf willow N and P concentrations were 43% and 52% higher, respectively, than for water sedge when averaged over the growing season. Digestibility of water sedge was 25% higher than that for planeleaf willow.

Season of grazing (i.e., late-spring, early-summer, late-summer, and fall) the

previous year did not affect forage quality in either species. Cattle use the previous year did, however, increase forage quality of water sedge as compared with plants that were not previously grazed. Grazed water sedge plants had higher concentrations of N and P and greater IVDMD than ungrazed controls ($p \leq 0.10$).

Nitrogen and P concentrations of browsed planeleaf willow were not different ($p > .10$) from controls, but IVDMD in browsed willow plants was 12% greater ($p \leq 0.10$) than those that were not browsed. The 2 species responded uniquely to cattle use, and this suggests that these life-forms differ in response to herbivory.

Total vegetation production primarily resulted from the growth of grasses and sedges. Total herbaceous production was greatest (330 g m^{-2}; $p \leq 0.10$) in paddocks that had previously been grazed in the spring or fall. Paddocks that had previously been grazed in the early-summer, or late-summer period produced approximately 240 g m^{-2} total herbaceous vegetation. Paddocks that had been previously grazed in the spring or fall produced about 20% greater standing crop of herbaceous vegetation than ungrazed control plots. The standing crop of dead plant litter on the soil surface averaged 650g m^{-2} in the control plots and was greatly reduced ($p \leq 0.10$) by any previous seasonal grazing treatment. This study supported the hypothesis that previous cattle use can improve forage quality and quantity in a riparian ecosystem.

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CHAPTER 1

FORAGE QUALITY

INTRODUCTION

The direct and indirect effects of livestock grazing on riparian ecosystems have become important topics of study as evidence of degradation and vegetation changes along streambanks in the western United States has accumulated (Platts and Nelson 1985). Many other factors may also be associated with these changes, including road development, recreation, timber harvest, and construction (Bryant 1982). The combinations of activities make it difficult to determine the effect of any particular activity on riparian components (Roath and Krueger 1982). Identification of precise cause and effect relationships will help riparian area managers and users become better stewards of these sensitive and valuable areas. Researchers and managers alike are interested in how large, vertebrate grazers change the riparian landscape and associated properties like streambank integrity, soil compaction, erosion, and vegetation structure and composition.

Studies have shown that large herbivores utilize riparian areas disproportionately heavy relative to upland areas (Roath and Krueger 1982, Platts and Nelson 1985). Therefore, identifying the impacts that domestic livestock have, and factors that influence their use and distribution, would be helpful. It is expected that heavy grazing might change plant species composition, production, stand density, vigor, and seed production (Ryder 1980). Some riparian vegetation responses to specific grazing regimes have been observed (Kauffman et al. 1983, Skovlin 1984, Platts and Nelson 1985, Schulz and Leininger 1990, Popolizio et al 1994, Clary 1995). These studies have examined changes in vegetation biomass, height, composition, and cover. Additional information is needed for better management of riparian grazing systems to indicate how livestock affect forage quantity and quality in riparian ecosystems (Platts 1986, Krueper 1996). Nutritive quality of forage

species following grazing has not been determined for montane riparian ecosystems.

The following questions were addressed in this study. (1) Does grazing or browsing affect nitrogen (N) and phosphorous (P) concentrations, or *in-vitro* dry-matter digestibilities (IVDMD) of riparian species? (2) Will the season of grazing influence nutritive properties of plants after being grazed or browsed? (3) How does seasonal changes in N, P and IVDMD in herbaceous and willow species interact with season of grazing?

Two common riparian species, that represented 2 different life forms, were chosen to study. A sedge, water sedge (*Carex aquatilus* Wahlenb.), and a woody species, planeleaf willow (*Salix planifolia* Pursh.), were selected as important montane riparian species and utilized in this study.

The purpose of this research was to determine how previous cattle use affected aboveground N and P concentrations and IVDMD at 4 phenological stages of plant development the year after short-term, high intensity grazing treatments. Significant differences in N, P and IVDMD among treatments were expected for water sedge. It was hypothesized that water sedge would have increased N concentration in current year's growth after grazing along with concomitant levels of increased P and digestibility. Other researchers have reported elevated N concentrations for upland graminoid species within weeks after defoliation (Ruess et al. 1983, Jaramillo and Detling 1988, Polley and Detling 1990, Rhodes and Sharrow 1990, Milchunas et al. 1995). This study, however, was conducted 8-12 months after grazing, and riparian rather than upland species were utilized. Unique riparian species and longer temporal scales distinguish this research from previous studies.

Forage quality changes in the willow were not expected to be as definitive as changes in the sedge, for there is little conclusive evidence to show that browsing has a discernible effect on N content or dry-matter digestibility of shrubs (Rhodes and Sharrow

1990). Planeleaf willow was browsed most heavily by cattle in the late-summer and fall (Pelster et al. 1996), so if there was evidence of a browsing effect, it was expected to be found among these seasonal treatments.

MATERIALS AND METHODS

Study Site

The Sheep Creek Allotment is located in north central Colorado, 80 km northwest of Fort Collins, within the Roosevelt National Forest at an elevation of approximately 2500 m. The Allotment consists of 5340 ha with 1050 ha classified as grazeable range. The riparian area was heavily grazed from the 1890's to the mid 1950's, according to U.S. Forest Service records. Three exclosures comprising 40 ha and 2.5 km of stream and adjacent riparian meadows were constructed in 1956 to exclude cattle use (Schulz and Leininger 1990, Popolizio et al. 1994). The study plots (paddocks) were located within these exclosures that had been protected for 40 years.

The nearest weather station to Sheep Creek is located at Red Feather Lakes, 15 km southeast of the study site at an elevation of 2542 m. Average annual long-term precipitation at Red Feather Lakes is 406 mm, while average long-term precipitation for the growing season (May-September) is 236 mm. Average long-term daily temperatures range from -11° C in January to 25° C in July, and average long-term daily temperatures during the growing season range from 0° to 25° C (National Climatic Data Center 1948-1990). For the study period (1995-1996), average growing season precipitation at the Red Feather weather station was 285 mm (21% above normal), and temperatures ranged from 4° to 16° C (NOAA 1996).

The Naz soil series dominates the Sheep Creek region. These are deep, well drained soils formed from granitic parent material. Soils in the riparian zones are primarily Naz 70, with 3 to 25% slopes. Texture of the series is sandy to clay loam and are classified as coarse loamy pachic cryoborols. The surface layer is an A horizon, consisting

of dark to gray-brown color. The A horizon ranges from 20 to 80 cm thick (USDA 1980).

Overstory vegetation at the study site was dominated by planeleaf willow, Geyer willow (*S. geyeriana* Anderss.), and yellow willow (*S. lütea* Nutt.). The understory herbaceous vegetation consisted of Kentucky bluegrass (*Poa pratensis* L.), fowl bluegrass (*P. palustris* L.), water sedge, Nebraska sedge (*C. nebraskensis* Dewey), beaked sedge (*C. rostrata* Stokes), tufted hairgrass (*Deschampsia caespitosa* L.), bluejoint reedgrass (*Calamagrostis canadensis* Michx.), and dandelion (*Taxaxacum officinale* Wiggers) (Schulz and Leininger 1991, Popolizio et al. 1994).

Methods

Small (0.25 ha) paddocks utilized in this study were randomly selected from suitable sites inside the exclosures mentioned above. Short-duration, high-intensity, seasonal grazing treatments with steers were applied in these paddocks in 1995. A set of 3 replicated paddocks that represented 1 of 5 grazing treatments; late-spring, early-summer, late-summer, fall, and control (not grazed) were assigned at random to the paddocks. Steers were placed in the designated paddocks at the beginning of each season and allowed to graze until herbaceous utilization reached approximately 65% (Pelster et al. 1996). Twelve plots were grazed similarly; the variation among them was in the time of the year (season) that they were grazed. Utilization levels were estimated to be about 65% of herbaceous biomass, according to the stubble-height measurement technique by Kinney and Clary (1994). Differences in species preferences at different seasons were determined while grazing treatments were imposed in 1995 (Pelster et al. 1996), and forage quality in the 2 contrasting species were determined the following year.

Random samples were taken of current year's growth for both species within each paddock during 4 times over the course of the 1996 growing season. Initial forage samples were gathered from all paddocks June 1 and represented early-spring growth. Early-

summer, late-summer, and fall samples were taken at the beginning of each successive month thereafter through September 1, 1996. Current year's growth of leaves and the tips of stems from planeleaf willow shrubs that were less than 2 m high were collected throughout each paddock. Water sedge plants were clipped at ground level at random within each paddock as well. A total of 60 samples for each species were collected throughout the growing season.

Forage samples were placed in paper bags, oven-dried at 50° C , weighed, and ground through a 1-mm mesh screen. Carbon and nitrogen contents were determined using a LECO CHN-1000 instrument (LECO Corp. 1993). The phosphorous analysis consisted of ashing samples in a muffle furnace at 500° C, performing an acid digest, and analyzing the digest with an inductively coupled plasma atomic emissions spectrometer (Baker et al. 1964). IVDMD was determined following the procedure of Tilley and Terry (1963), as modified by Pearson (1970). Samples were inoculated with rumen fluid obtained from a fistulated steer and allowed to digest in test tubes for 48 hours at 39° C. This was followed by an acid pepsin digest for an additional 48 hours to simulate digestion of material leaving the rumen.

All data were analyzed using analysis of variance techniques for a completely randomized block design with repeated measures in a factorial arrangement of treatments. Data for each species were analyzed separately using the SAS (1996) general linear models procedure. The main effects tested were previous grazing treatments and collection times. A repeated measures procedure through time was used to determine significant effects ($p<0.10$) of collection time, species, grazing treatment, and collection time by grazing treatment interactions. A univariate procedure with collection time and grazing treatment as dependent variables was also utilized. Furthermore, differences between grazed plants versus those that were not grazed were compared using a contrast statement (SAS 1996). Stepwise and simple linear regression analyses were also used to determine if relationships

between digestibility, nitrogen and phosphorous concentrations, and carbon:nitrogen (C:N) ratios existed for each of the 2 species (SAS 1996).

RESULTS

Nitrogen and phosphorous concentrations and IVDMD were measured repeatedly a the beginning of each month from June to September 1996. Collection times represented seasons that also correspond, respectively, with 1995 grazing treatments: late-spring, early-summer, late-summer, and fall. Over the course of the 1996 growing season, time o sample collection was a significant factor ($p<0.0001$) for each of the three variables measured in both species (Appendix Table 1). Nitrogen and P concentrations and IVDMD averaged across all grazing treatments plus controls, decreased in both water sedge and planeleaf willow as phenological development continued from young leaves and shoots to senescence.

Nitrogen

A repeated measures analysis of variance for N concentrations in water sedge and planeleaf willow indicated that this variable was not affected ($p>0.10$) by the season of cattle use one year after plants were grazed (Appendix Table 3). Season of grazing treatment did not affect N concentrations, and there were no significant collection time by grazing treatment interactions for N in either species ($p>0.10$) (Appendix Table 2).

A univariate analysis that contrasted grazed versus ungrazed plants over all collection times was used to determine if previous cattle use affected forage quality the nex year. This linear contrast showed that grazed water sedge N concentrations were significantly greater ($p\leq0.10$) compared with plants that were not previously grazed (Appendix Table 4). Nitrogen in grazed water sedge was 5% to 10% higher than in

comparable ungrazed plants (Figure 1). Grazed water sedge plants remained higher in N than ungrazed plants throughout the growing season, but the greatest difference occurred i late-spring. Nitrogen concentrations between browsed and unbrowsed shrubs, on the other hand, were not significantly different ($p>0.10$) over all collection times the year after grazing treatments were applied (Appendix Table 4).

Nitrogen concentrations declined as phenology of water sedge and planeleaf willow advanced ($p<0.0001$). Averaged across all grazing treatments and controls, water sedge N concentration averaged 2.5% on June 1. This value declined approximately 20% each successive month thereafter to 1.3% N on September 1. Planeleaf willow N concentration also decreased each month ($p<0.0001$) and ranged from a high of 3.3% on June 1 to a low of 2.1% on September 1 (Figure 1). This gradual decline from one month to the next was similar for both species and reflected seasonal, phenotypic dynamics.

Nitrogen concentrations were also significantly different ($p<0.0001$) between water sedge and planeleaf willow (Appendix Table 5). Planeleaf willow contained an average (al grazing treatments plus controls) of 43% more forage N than did water sedge.

Phosphorous

A repeated measures analysis of variance for P concentrations in water sedge and planeleaf willow indicated that collection time by grazing treatment interactions were not significant for either species (Appendix Table 2). Season of grazing, also, did not affect P concentration ($p>0.10$), with the exception of the late-summer collection time (Appendix Table 3). In the August collection, plants that had been grazed or browsed in the late-spring were found to be higher ($p>0.10$) in P concentration as compared with other seasonal grazing treatments for both species. With this exception, season of cattle use did not significantly affect P concentration over the course of the next growing season.

A univariate analysis that contrasted grazed versus ungrazed plants over all

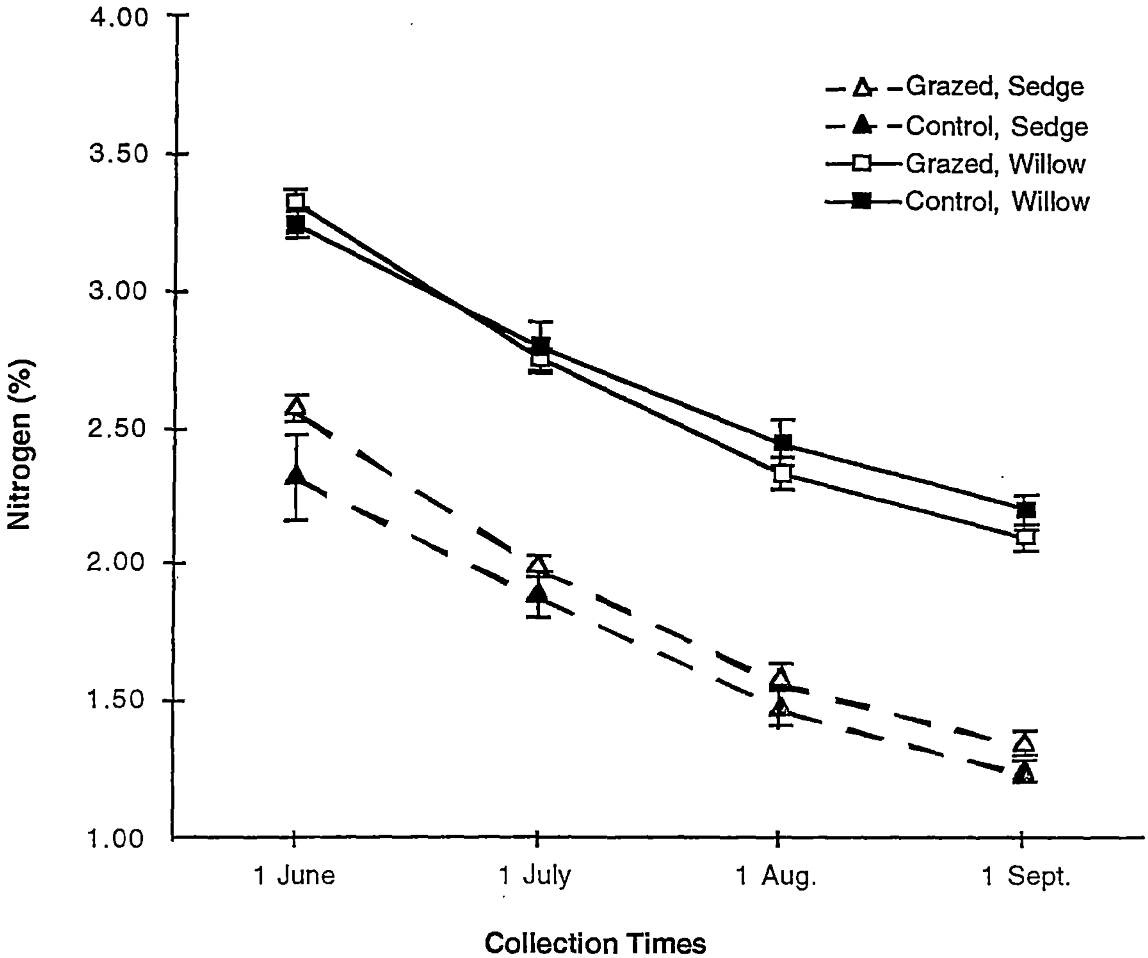

Figure 1. Nitrogen concentration in current year's growth for grazed and ungrazed plants of two riparian species, water sedge (*Carex aquatilus*) and planeleaf willow (*Salix planifolia*). Data points represent means (± standard error) for the dates that samples were collected. Collection times correspond with the following seasons: late-spring (June 1), early-summer (July 1), late-summer (Aug. 1), and fall (Sept. 1).

collection times was used to determine if previous cattle use affected forage quality the next year. This linear contrast showed that grazed water sedge P concentrations were significantly greater ($p \leq 0.10$) compared with plants that were not previously grazed (Appendix Table 4). Phosphorous concentrations were 14% higher in grazed than in ungrazed plants at the beginning of the growing season (Figure 2). This differential declined from about 12% in July and August to <1% in September. Thus, the effect of grazing on water sedge leaf P concentration diminished by the end of the growing season. Browsed planeleaf willow, on the other hand, showed no significant differences ($p>0.10$) in P concentrations over all collection times as compared with plants that had not been browsed the previous year (Appendix Table 4).

Phosphorous concentrations also declined seasonally ($p<0.0001$) for both species, as depicted in Figure 2. Phosphorous values for water sedge, averaged across all grazing treatments and controls, decreased each month from a high of 0.34% on June 1 to a low of 0.11% on September 1. Planeleaf willow average P value began at 0.52% on June 1 and by the end of the growing season was at 0.19% on September 1 (Figure 2). The seasonal low of 0.16%, however, was found in August. Average P concentrations declined most dramatically (>50%) between early-summer and late-summer, whereas the change between late-summer and fall was not significant ($p>0.10$).

Water sedge and planeleaf willow P concentrations were also significantly different ($p<0.0001$) from one another (Appendix Table 5). Planeleaf willow contained an average (all grazing treatments plus controls) of 52% more foliar P than water sedge. Water sedge N and P concentrations were highly correlated ($r=0.91$), but this was not the case for planeleaf willow ($r=.10$). The gradual seasonal decline found in water sedge P concentration did not parallel the steep decline found in planeleaf willow P concentration. A grazing treatment x species x time of sampling 3-way interaction was found for P (Appendix Table 5), and this may be explained by differences in seasonal dynamics

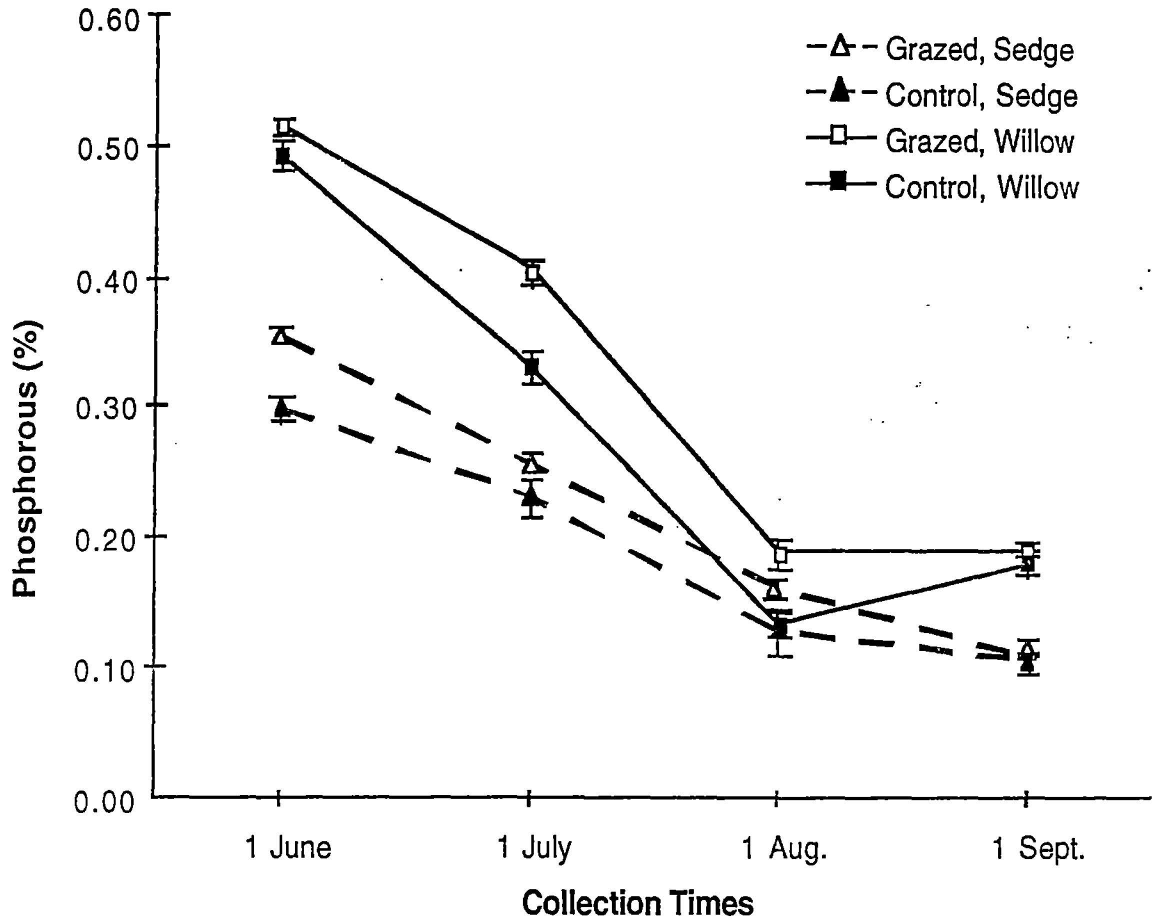

Figure 2. Phosphorous concentration in current year's growth for grazed and ungrazed plants of two riparian species, water sedge (*Carex aquatilus*) and planeleaf willow (*Salix planifolia*). Data points represent means ($\pm$ standard error) for the dates that samples were collected. Collection times correspond with the following seasons: late-spring (June 1), early- summer (July 1), late-summer (Aug. 1), and fall (Sept. 1).

between species that caused the interaction to be significant ($p<0.0001$). The decline in P concentration in willow plants between July and August was greater than that found for water sedge. Also, differences in P between browsed and unbrowsed willow plants during the summer were greater, as compared with grazed and ungrazed water sedge plants. These data reflect distinctive species-level responses among seasons that contributed to the significant 3-way interaction.

In-Vitro Dry-Matter Digestibility

A repeated measures analysis for IVDMD in water sedge indicated that seasonal grazing treatments and collection time by grazing treatment interaction were not significant ($p>0.10$). A grazing treatment effect ($p<0.10$) was found in the fall collection for water sedge, but this isolated case was outweighed by the lack of seasonal grazing treatment effects for plants collected in June, July, and August (Appendix Table 3). In the case of planeleaf willow IVDMD, there was a significant ($p<0.0001$) collection time by browsing treatment interaction (Appendix Table 2). In addition, browsing treatments significantly affected willow IVDMD ($p<0.10$) at the June, August, and September collection times (Appendix Table 3). Thus, effects of previous browsing were not uniform through time. Effects of cattle use found in late-spring, late-summer, and fall for planeleaf willow were not evident in early-summer (Figure 3). IVDMD for willow that were browsed during any season the previous year were found to be statistically different from those that were not browsed in the June, August, and September collections. All browsed plants were higher in digestibility than unbrowsed plants in the June and September collections, while unbrowsed plants were more digestible than those that were browsed at any season the previous year in the August collection. A browsing treatment difference was not found in July, and the browsing treatment effects found through time were primarily associated with the overall effects of browsing when compared with unbrowsed plants.

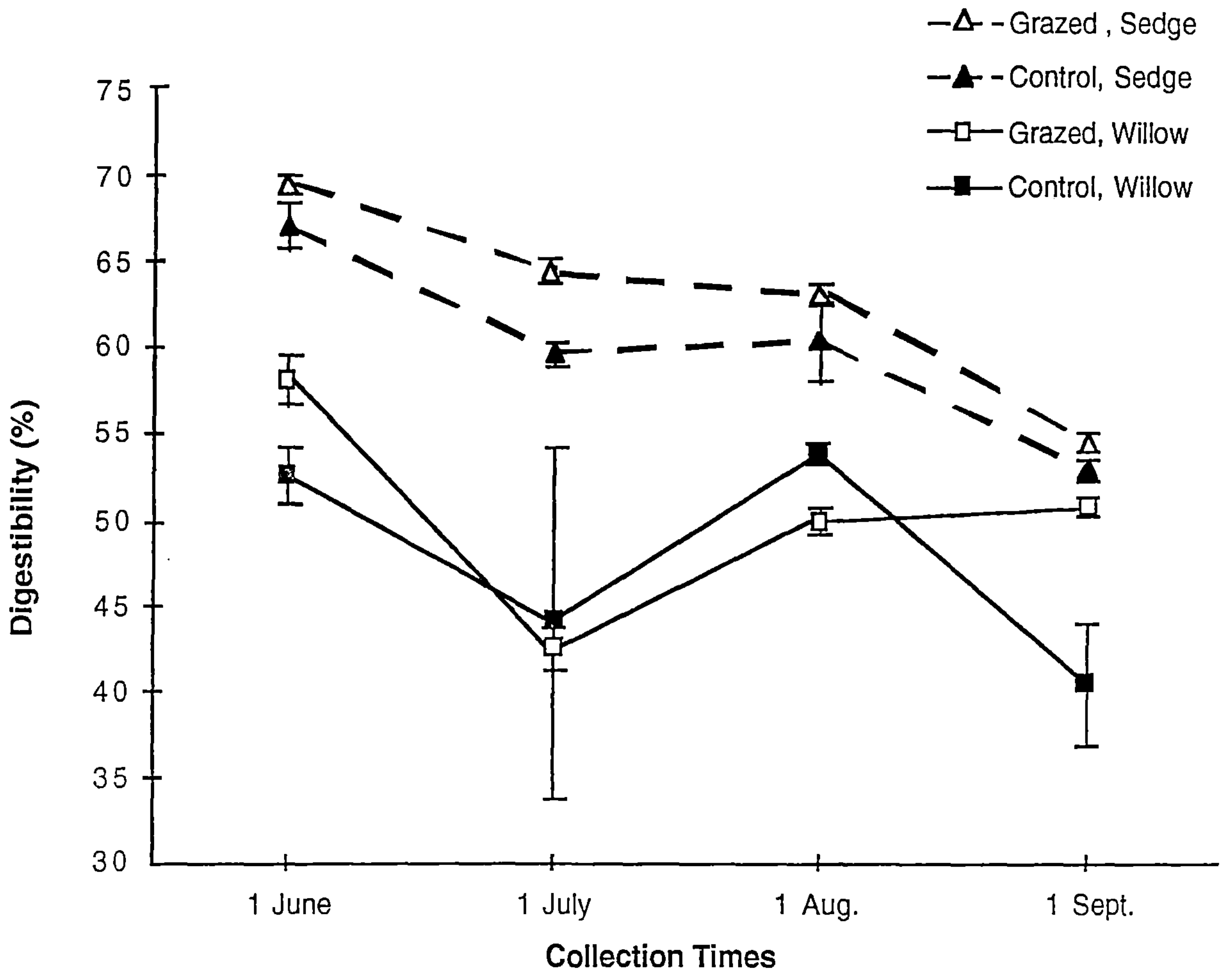

Figure 3. Digestibility in current year's growth for grazed and ungrazed plants of two riparian species, water sedge (*Carex aquatilus*) and planeleaf willow (*Salix planifolia*). Data points represent means (± standard error) for the dates that samples were collected. Collection times correspond with the following seasons: late-spring (June 1), early-summer (July 1), late-summer (Aug. 1), and fall (Sept. 1).

A univariate analysis that contrasted grazed versus ungrazed plants was used to determine if previous cattle use affected forage quality the next year (Appendix Table 4). This linear contrast showed that IVDMD in grazed water sedge plants was significantly greater ($p \leq 0.10$) than in plants that were not previously grazed (Figure 3). Differences from 2.9 to 6.3% were found between grazed and ungrazed water sedge, and grazed plants had consistently higher IVDMD at each collection time than did ungrazed plants. This linear contrast also indicated that IVDMD of browsed planeleaf willow was greater ($p \leq 0.10$) over all collection times than those plants that had not been used by cattle the previous year (Appendix Table 4). Greatest differences were found in the late-spring and fall, when browsed willows were 5.5% and 11% more digestible than those plants that had not been browsed (Figure 3).

Like N and P, IVDMD also declined seasonally ($p<0.0001$) for both species (Appendix Table 1). Average IVDMD for water sedge, including all grazing treatments and controls, ranged from 68% in early-spring to 54% in the fall (Figure 3). Water sedge IVDMD, however, did not decline as linearly as did N and P. Sharp declines in IVDMD were found in the differences between late-spring and early-summer samples (7%) and between late-summer and fall samples (12%). The decline in water sedge IVDMD between early-summer and late-summer, however, was only 1.6%. Digestibility values between early and late summer remained about 63% during mid-season. These data indicate how water sedge IVDMD could not be predicted from N and P data alone, since seasonal patterns of N and P did not parallel IVDMD. A stepwise linear regression model, however, did show a significant relationship ($p<0.0001$) between C:N ratio of water sedge and IVDMD, with an r^2 of 0.61 (Figure 4).

Seasonal declines in IVDMD for planeleaf willow were also evident, although the trend throughout the growing season was not linear. Average IVDMD across all browsing

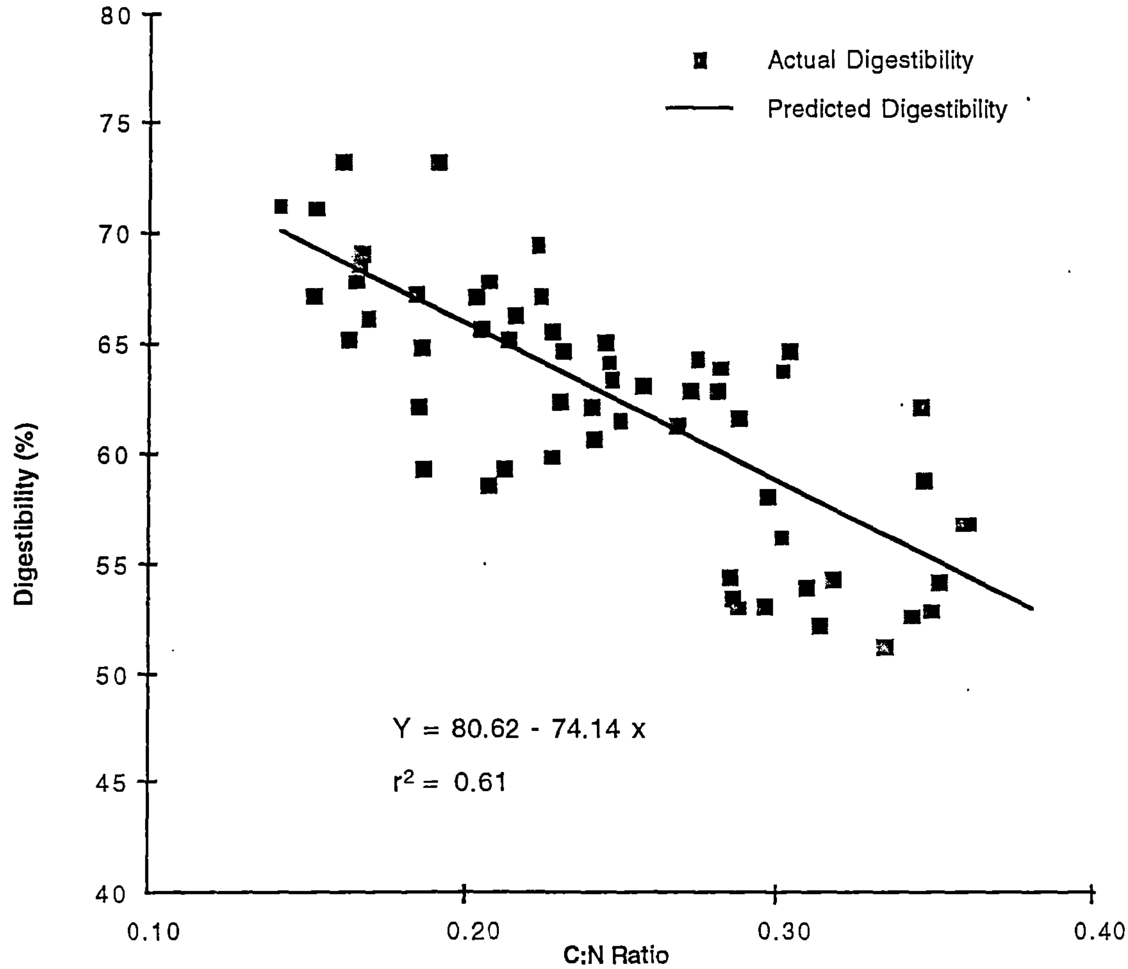

Figure 4. Linear regression analysis of C:N ratio and digestibility for water sedge (*Carex aquatilus*). Data for all treatments and collection times are included in this analysis.

treatments plus controls for willow began at 56% in late-spring and ended at 47% in the fall. Lowest average IVDMD of 43%, however, was found in early-summer. This value rebounded in late-summer to 51%, which was similar to the average IVDMD found for water sedge in the fall. Digestibility of planeleaf willow did not parallel seasonal N and P concentrations. This may be one reason why the forage quality indicators measured for planeleaf willow were inadequate predictors of digestibility using a stepwise linear regression model.

Water sedge and planeleaf willow IVDMD were also significantly different ($p<0.0001$) from one another (Appendix Table 1). Digestibility of water sedge was approximately 25% higher than that of planeleaf willow. Willow IVDMD also varied more through time than the gradual changes found in water sedge (Figure 3). Like phosphorous, a grazing treatment x species x time of sample collection 3-way interaction was found for digestibility (Appendix Table 5). This interaction may also be explained by the seasonal IVDMD differences in water sedge versus those found in planeleaf willow. Water sedge average IVDMD leveled off over the summer, while planeleaf willow IVDMD spiked upward between July and August. These seasonal species-level differences caused the 3-way interaction to be significant ($p<0.01$).

Species Comparisons

Species-level differences were found as a result of varying effects that cattle use had on forage quality. Concentrations of N and P increased along with IVDMD in forage of water sedge as a result of previous grazing, while only IVDMD increased in planeleaf willow foliage the year following cattle use. The greatest increase in water sedge digestibility from grazed plants compared with controls was found in early-summer, while the greatest difference in willow digestibility was found in the fall. Grazed water sedge N and P concentrations were consistently higher than ungrazed control plants each season,

while planeleaf willow N and P concentrations did not change from late-spring to fall as a result of browsing the previous year.

Ash-free weights of the water sedge were not significantly different ($p>0.10$) among grazing treatments or collection times, and this was also true for planeleaf willow. Average water sedge organic matter content was 92%, while planeleaf willow organic matter content averaged 94%. These small differences did not warrant expressing data for N, P, and IVDMD for the 2 species on an ash-free basis.

DISCUSSION

Water Sedge

Water sedge nutritive characteristics varied seasonally, and comparative research that includes riparian forage quality data throughout an entire growing season is lacking. Coppock et al. (1979) determined %N and IVDMD for *Carex* spp. from May to October, and these data are similar to those found in this study. Coppock et al. (1979) reported N concentrations from 1.0 to 1.7% and IVDMD values from 52 to 63% over the growing season for *Carex* spp. in a mixed-grass prairie. Researchers at the Central Plains Experimental Range (CPER) determined N concentration and IVDMD for *Bouteloua gracilis* (H.B.K.) dominated forage in the short-grass prairie (Milchunas et al. 1995). Milchunas et al. (1995) found that forage harvested at peak standing crop (September 1) contained about 1.8% N and were 60-65% digestible. Results from other clipping studies include work with *Kyllinga nervosa* (Steud.), a native of the Serengeti National Park in Tanzania. Nitrogen concentrations of 2-3% and P concentrations of 0.2% have been reported for *K. nervosa* (McNaughton and Chapin 1985), and these data are within the range reported for water sedge in the present study.

The higher forage quality found in grazed water sedge as compared with controls is in agreement with several greenhouse and field experiments where other defoliated graminoids have been studied (Coppock et al. 1983, Ruess 1984, Ruess and McNaughton 1984, McNaughton and Chapin 1985, Jaramillo and Detling 1988, Polley and Detling 1988 Milchunas et al. 1995). These researchers, however, measured results within the same season of treatment and this may be evidence of how intensive grazing or clipping removes

older growth and facilitates the subsequent replacement by younger tissue with lower C:N ratios (Jameson 1963, Kamstra et al. 1968). Data for this study were gathered the year following cattle use, so samples for both grazed and ungrazed plants represented current year's growth that was not grazed or browsed the year of collection. Other comparable results are not available, so I suggest that these protracted responses may be attributed to water sedge nutrient storage strategies, accelerated mineralization in soils of grazed paddocks and increased nutrient availability, or altered riparian nutrient-cycling dynamics in grazed paddocks.

Defoliation-induced increases in foliar N and P concentrations have been linked to higher nutrient uptake rates (Chapin and Slack 1979, McNaughton and Chapin 1985, Jaramillo and Detling 1988, Polley and Detling 1989, Coughenour 1991). These accelerated uptake rates have been attributed to increased mineralization or nutrient availability (Holland and Detling 1990, Seagle et al. 1992), changes in root affinity (McNaughton & Chapin 1985), as well as possible hormonal effects (Coughenour 1991). I did not measure nutrient uptake rates in this experiment, but increased uptake in the grazed water sedge might be inferred by the results obtained. Growth and storage adaptations necessary in this montane habitat must be considered in the context of uptake and allocation because nutrient storage is an essential feature of this graminoid (Chapin and Bloom 1976). Aboveground and belowground patterns of nutrient supply and demand by water sedge are temporally decoupled. Temperatures and moisture favorable for photosynthesis and shoot growth are often found while the soil is still frozen, so root growth and function probably lags behind shoot growth.

Chapin and Bloom (1976) believed that nutrients absorbed by water sedge after the end of July would not be fully utilized until the following spring. Elevated levels of leaf N, P, and IVDMD the year following grazing might be explained by nutrient storage patterns in water sedge. If uptake were stimulated by cattle use, either through increased nutrient

availability or by hormonally mediated uptake mechanisms, some of the luxury uptake accumulated in late 1995 may have been stored over the winter and allocated to aboveground biomass in 1996.

Use by cattle may have increased forage quality by directly and indirectly changing the availability of nutrients to plants and microorganisms (Ruess and McNaughton 1987, Seagle et al. 1992). Forage removal and the subsequent return of decomposable material to the soil surface by cattle in forms more readily useable by plants and microorganisms accelerates nutrient turnover (Ruess et al. 1983, Ruess 1984). Dung and urine depositions can substantially increase the soil mineral nitrogen pool; potentially affecting microbial biomass, C:N ratios, and plant uptake (McNaughton 1985, Ruess 1987, Seagle et al. 1992). Also, grazing decreases litter accumulation in productive riparian communities (Popolizio et al. 1994). Reductions in litter cover were found among these grazing treatments in 1997 compared with ungrazed controls (Schenck, personal communication). Less litter would allow greater penetration of solar radiation and higher soil temperatures. This in turn would lead to greater rates of decomposition (Knapp & Seastedt 1986, Ruess 1987). Increased leaf N and P concentrations may be evidence of increased soil nutrient availability, ultimately controlled by accelerated nutrient turnover rates.

This rationale is ostensibly predicated by the notion of nutrient limitation, or a N-limited system. The salient question is whether or not cattle use changed the soil nutrient status of the water sedge community. The soil nutrient status at Sheep Creek is not known, but belowground processes characteristic of riparian areas are important to this question. Soils typically found along riparian corridors are high in organic matter, saturated with water, and low in oxygen and redox potential (Green and Kauffman 1989). These conditions are ideal for anaerobic microorganisms. Anaerobic nutrient reduction follows a predictable pattern beginning with nitrate-nitrogen (NO_3^-), that is reduced to form N_2O, N_2, NO_2^-, and NH_4^+. These conditions may accelerate competition for available N as both

plants and microorganisms take up NO_3^- ions, especially under saturated conditions. Functionally intact riparian areas have been found to function as important sites for denitrification (Lowrance et al. 1984), so this process of denitrification may contribute to unavailability of soil N. In this case, competition between plants and the microbial community for essential elements would be eased by nitrogenous cattle depositions, higher mineralization rates, and lower plant C:N ratios as discussed. Increased N and P concentrations and IVDMD in water sedge is evidence that cattle use affected belowground nutrient dynamics, although the precise mechanisms are subjects of conjecture. The denitrification process may be an important link towards understanding competition for nutrients among plants and microorganisms in riparian areas. A greater understanding of nutrient limitation and competitive potential in the field should help determine how availability, uptake, herbivory, and decomposition contribute to increased forage quality.

Further field studies are needed to determine spatial and temporal variations in riparian nutrient dynamics and the extent of graminoid responses to herbivory. Ideally, a long-term study would include data collection prior to defoliation, during regrowth that season, and in new growth the following year. This experiment represents data for one growing season that encompassed only a community-level spatial scale in a montane riparian ecosystem. Clarification of how compensatory nutrient uptake and allocation patterns operate requires species-level, ecophysiological approaches be used that explore mechanisms that affect these response variables in the context of highly interactive soil-plant ecology. Evidence of higher forage quality in this study suggests that grazing induced a change in available nutrients and nutrient uptake in water sedge. A quantitative understanding of the underlying, indirect mechanisms will require greater study of the riparian soil-plant nutrient exchange complex.

Planeleaf Willow

Planeleaf willow nutritive characteristics also vary seasonally, and comparative repeated measures data in the literature are lacking. Nitrogen and digestibility among browse species have been reported under natural and simulated browsing, but these data represent individual points in time and the browsing treatments varied considerably from this study. Nonetheless, this previous research does provide a framework for comparison. For example, nitrogen concentrations for *Betula pubescens* (Ehrh.) from 1.6 to 2.4% have been reported, along with pepsin/cellulase digestibility values of 48-49% (Danell and Huss-Dannell 1985). Forage quality variables have also been determined for *Salix* spp. in Yellowstone National Park (Singer et al. 1994). Singer et al. (1994) found nitrogen concentrations of 1-2% and dry-matter digestibility values from 45-53% for several willow species. These digestibility data are within range, but nitrogen values are lower than those found in this study. Willow nitrogen concentration varies significantly over time, so this discrepancy may be an artifact of the timing of sample collection.

Data for planeleaf willow N and P concentrations were reported at Sheep Creek from July-September 1994 and 1995 by Dernberg (1997). The P concentrations from leaf expansion to senescence were 0.32-0.27%, and N concentrations over the same time frame ranged from 2.4 to 1.8%. These values are slightly lower than those determined in this study, but Dernberg found that concentrations varied by a similar amount from 1994 to 1995.

Unlike water sedge, nutrient characteristics of browsed planeleaf willow plants were not significantly different from those of unbrowsed plants. Seasonal grazing treatment did not significantly affect foliar concentrations of N and P the following year. Planeleaf willow digestibility, however, was significantly higher in those shrubs that were

browsed the previous year as compared with unbrowsed controls. The increase in digestibility was independent of N and P concentrations, and neither N nor P were good predictors of digestibility in a linear regression model. These data contrasted with similar data for water sedge, where all 3 variables increased significantly in response to cattle use the previous year.

The contrasting responses between a riparian sedge and a woody-shrub are evidence of variability associated with plant life-forms that may represent adaptive strategies unique to each type of plant. Disparate strategies were demonstrated further by significant differences in N and P concentrations and IVDMD between the two species throughout the growing season. Furthermore, although this willow and sedge are commonly associated with western riparian ecosystems (Youngblood et al. 1985, Kovalchik 1987), their nutritive responses to cattle use varied significantly.

The same indirect effects of cattle use that we suspected may have contributed to elevated N, P, and IVDMD in grazed water sedge did not result in similar planeleaf willow responses. Potential increases in nutrient cycling rates and greater soil N and P availability in the top portion of the soil profile did not change foliar N and P in the shrub. Two broad-scale possibilities exist, given that soil nutrient availability increased as a result of cattle use. Either changes in nutrient availability did not affect the nutrient status of planeleaf willow, or else more available nutrients in the first few centimeters of soil were not available for uptake by the deeply rooted shrub. Of these two possibilities, the latter may offer the most plausible explanation for the contrasting responses to cattle use between the two species. Water sedge belowground biomass is greatest in the first 10 cm of soil (Ratliff and Westfall 1988), while the greatest proportion of willow root biomass extends deeper into the soil profile (Jolley, unpublished data). Differences in root distribution affects plant uptake and allocation, so the deep spatial distribution of planeleaf willow roots might have rendered the shrub ineffectual for absorption of surface-level nutrients. My

sampling design did not include root and stem measurements; consequently, I cannot determine whole-plant N and P concentrations changes from these data.

Forage quality differences have been reported to differ for some woody browse species as affected by defoliation intensities (Bryant 1981, Danell et al. 1985, Danell and Huss-Danell 1985, Singer et al. 1994). Moderate to high levels of browsing has resulted in increased leaf N and dry-matter digestibility (Danell and Huss-Danell 1985), lower IVDMD and tannins (Singer et al. 1994), and increased palatability (Danell et al. 1985) among woody species. Again, these responses were measured during the same growing season as when plants were browsed or under continuous use. These increases, then, may not be meaningful in comparison with results from this study when plant responses were measured in the growing season after browsing.

General theory, as well as these data, suggest planeleaf willow is more carbon- than nutrient-limited (Bryant et al. 1983). Along with being a mid-successional species adapted to more fertile habitats (Youngblood et al. 1985), foliar N and P concentrations did not change in response to cattle use. Instead, digestibility increased, which might suggest that levels of carbon-based, secondary or fibrous compounds were lower than in the ungrazed, less-digestible shrubs. Short-duration, high intensity cattle use in 1995 may have stressed carbohydrate reserves (Trlica 1977, Lamman 1995) and affected synthesis of recalcitrant or secondary compounds the following year. If planeleaf willow at this site is carbon-limited, leaf concentrations of secondary compounds may have declined in response to previous browsing. High levels of condensed tannins have been found in planeleaf willow at Sheep Creek (Hasting 1993), yet the chemical constituents that respond to defoliation have not been determined.

Season of use did not affect N, P, nor IVDMD in planeleaf willow and water sedge. All three variables were significantly higher in the grazed water sedge, but only IVDMD was higher in the browsed planeleaf willow. Determinants of planeleaf willow

digestibility are not known and are not correlated with foliar N and P. Detailed, comprehensive chemical assays may help determine which compounds are most affected by browsing and the relationship of these chemicals to willow digestibility.

CONCLUSIONS

Forage quality of water sedge and planeleaf willow was affected the year following short-term, high-intensity cattle grazing in a montane riparian ecosystem at Sheep Creek, and the disparate responses were indicative of ecophysiological mechanisms unique to each life-form. Increased N, P, and IVDMD in water sedge may be evidence of increased uptake kinetics, greater nutrient availability, or reallocation of reserves. Greater IVDMD in planeleaf willow, on the other hand, may suggest lowered levels of secondary compounds or fiber in a carbon-limited shrub.

Season of use did not affect forage quality, although season of use can affect other variables such as plant cover, production, and streambank erosion (Kauffman et al. 1983). These data demonstrated how grazing might affect growth the following year in a riparian area, compared with plants that were not used, thereby improving graminoid forage quality in the year following cattle use. Conclusions are based on these one time, short-term, high-intensity cattle use treatments at 4 periods during 1 growing season. Other cattle management regimes may not yield similar results. This study has demonstrated that previous cattle use can increase forage quality of a montane riparian community, although substantiation with studies at different spatial and temporal scales is recommended.

This study has shown that cattle use affects riparian vegetation, but the conspicuous question is how does grazing change the system? There is evidence from N-fertilization experiments of the lack of a foliar N increase in both a sedge and willow species (Bemhaja 1990, Bowman and Conant 1994). This might indicate that the fertilization effect of cattle deposition is insufficient to explain an increase in forage N. Increased N yield among defoliated prairie graminoids suggests greater nutrient uptake within a few weeks after

clipping (Ruess et al. 1983, Ruess 1984, McNaughton and Chapin 1985, Jaramillo and Detling 1988, Milchunas et al. 1995), but whether greater uptake would be found months after grazing has not been determined. I suggest that luxury nutrient uptake in water sedge, stimulated by cattle use, was stored and translocated aboveground the following season. Furthermore, greater mineralization rates in surface soil may have resulted in greater nutrient availability for shallow rooted plants. Additional studies of water sedge should include repeated measures from before the time of grazing treatment through at least 1 year after grazing, and should also include rates of soil processes along with plant uptake and nutrient storage data. Future research of planeleaf willow, on the other hand, might include the whole-plant carbon status under browsing or more work with secondary and fibrous compounds. With both species, however, research of hormonal signals that are stimulated by grazing and browsing should yield valuable information about how herbivory alters plant foliar chemistry.

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CHAPTER 2

FORAGE PRODUCTION

INTRODUCTION AND PROBLEM STATEMENT

During the past decade, there has been increasing concern over the impact of livestock grazing on streamside vegetation (Huber et al. 1995, Belsky and Matzke 1999). This concern is particularly evident on public lands in the western United States. Livestock grazing may induce a number of biotic and abiotic responses in a riparian ecosystem. The magnitude and direction of these effects vary according to factors such as site, climate, time of grazing, soil, vegetation and regional history. As Clary (1995) stated, riparian areas have responded irregularly and unpredictably to many grazing systems that have been developed and tested on upland rangeland. Although much data have been gathered from ongoing studies in lower elevation grasslands (Bedunah and Soesebee 1995), there are still ecosystems that lack complimentary, complete data sets. The higher elevation (>2000m) riparian zone is one such system that needs further research to quantify how grazing might specifically impact streambank vegetation dynamics and whether these impacts are similar to those on other rangelands. This proposed project is an extension of two research projects that were initiated in 1994 and 1995 to evaluate the seasonal diets of cattle grazing mountainous riparian zones (Evans et al. 1996 and Pelster et al. 1996).

The primary objective of this portion of the study is to compare the forage production in riparian sites that had been protected from livestock grazing for 28 years with sites that had received grazing the previous year at four phenological growth stages.

JUSTIFICATION

Riparian zones serve as critical linkages between in stream aquatic and terrestrial ecosystems (Green and Kauffman 1995). Even though they typically comprise less than 1% of the land base in the western U.S., these ecosystems provide critical habitat for more species of breeding birds than any other type in the western U.S. (Knopf and Samson 1994). It is widely believed that the riparian ecosystem is the single most productive type of terrestrial wildlife habitat, benefitting the greatest number of species (Ames 1977, Patton 1977, Kauffman and Krueger 1984, Schulz and Leininger 1991, and others).

In 1988 the General Accounting Office (GAO) noted that of Colorado's riparian areas under Bureau of Land Management stewardship, 51% was in poor condition, 39% was in fair condition, and only 10% was in good condition. Nationally, the U.S. Council on Environmental Quality (1978) estimated that America had lost between 70 and 90% of its riparian resources, while having badly damaged much of the rest. Although livestock grazing is generally considered to have had the greatest impact on riparian systems in the western U.S., there is a lack of data necessary to quantitatively support the development of sound grazing practices. Research is needed to understand how grazing changes, reduces, or eliminates vegetation bordering a stream (Platts 1981). This study should serve two purposes: First, to help managers of riparian areas to better understand the resilience of a montane riparian ecosystem to different levels of use during different times of the year. Second, to evaluate the role of livestock grazing in wet meadows as it

pertains to herbaceous forage production. These findings, coupled with those from Chapter 1 on the impacts of gazing on forage quality will help land managers in developing grazing management plans for riparian areas.

MATERIALS AND METHODS

The same grazing paddocks that were used in the previous study on forage quality were also used in this study on forage production. Aboveground production for grasses, sedges, forbs, total vegetation, and litter was collected in the 1996 growing season following completion of the 1995 grazing trials. These data were collected at peak standing crop during the growing season to determine the effects of previous grazing at different seasons on aboveground biomass production. Thirty 0.25 m^{-2} quadrats within each paddock were clipped to ground level, oven-dried at 50° C and weighed to the nearest .10g. Only current year's growth of herbaceous species was sampled, and vegetation within clipped plots was separated by major life forms.

The experiment was a randomized complete block design and data were analyzed using analysis of variance procedures. When significant ($p \leq 0.05$) differences in treatments and interactions were detected, significant means were then separated using Fisher's Least Significant Difference procedure.

RESULTS AND DISCUSSION

A significant ($P \leq .05$) season by vegetation category interaction was found, therefore, main effects will not be discussed. Grasses were more productive in the control (not grazed) and early- summer grazing treatments than in the three other grazing treatments (Fig. 5). However, sedges were most productive in the fall and spring grazing treatments and numerically the least productive in the early-summer grazing treatment. Total graminoid (i.e., grasses and sedges) production in the fall grazing treatment was approximately 300 g m^{-2} compared to only 250 g m^{-2} in the control. Forb production was low in all plots (< 50 g m^{-2}), however forb standing crop was highest in the late summer grazing treatment. Production of forbs was the lowest in paddocks that had been grazed in the previous spring.

Total vegetation production primarily resulted from the growth of grasses and sedges. Total herbaceous production was greatest (330 g m^{-2}; $p \leq 0.10$) in paddocks that had previously been grazed in the spring or fall. Paddocks that had previously been grazed in the early-summer or late-summer period produced approximately 240 g m^{-2} total herbaceous vegetation. Therefore, total vegetation production mimicked production trends found for sedges, as sedges dominated the herbaceous understory. Paddocks that had been previously grazed in the spring or fall produced about 20% greater standing crop of herbaceous vegetation than ungrazed control plots. It is important to note that an increase of 20% in vegetation production on paddocks that had previously been grazed

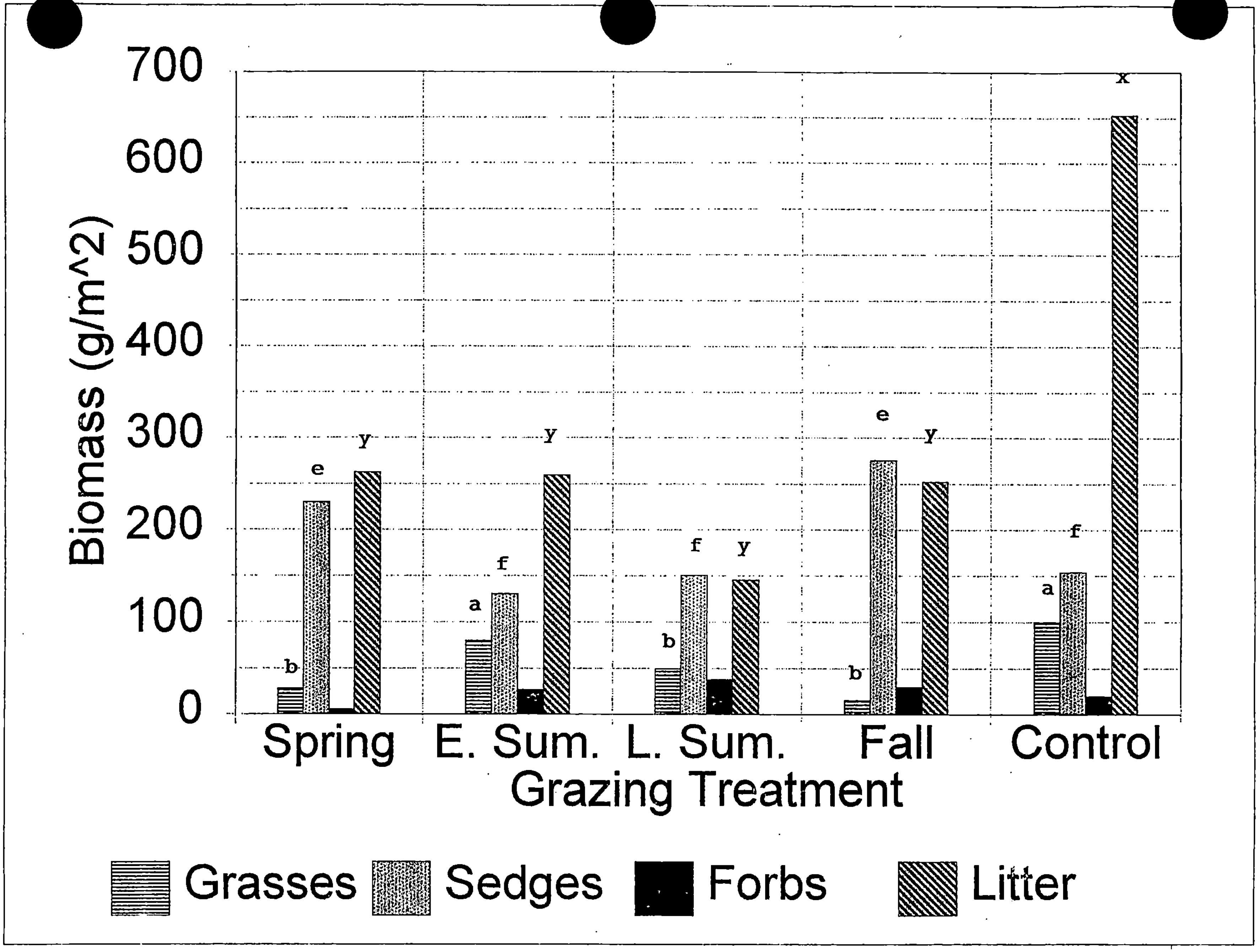

Figure 5. Peak standing crop (g m^{-2}) for paddocks grazed the previous year during 4 seasons at Sheep Creek. Means with the same letter are not different at P> .05 level of significance.

(Fig. 5) is a large increase in production as a result of previous grazing. Phillips et. al. (1998) found that the highly productive sedge, *Carex aquatilis,* also had greater concentrations of nitrogen and phosphorus and were more digestible than plants that had not been previously grazed.

The standing crop of dead plant litter on the soil surface averaged 650 g m^{-2} in the control plots and was greatly reduced by any previous seasonal grazing treatment (Fig. 5). With more bare soil present in previously grazed paddocks, soil temperature and water relations were probably affected. We believe that surface soils in grazed treatments warmed up more, had greater evaporation, and higher decomposition and mineralization rates than did soils of ungrazed paddocks. Evidently the sedges could take advantage of this microenvironmenal change and responded with increased production and nitrogen uptake. What is now needed is a study of litter decomposition, nitrogen mineralization, and plant nitrogen uptake in grazed and ungrazed riparian communities to determine interactions of grazing with the nitrogen cycle.

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APPENDIX

Appendix Table 1. Analysis of variance for the influence of sample collection time on N and P concentrations and digestibility (IVDMD) for current year's growth of water sedge and planeleaf willow. Tests of the hypotheses that time of sampling did not affect each variable were conducted using a repeated measures analysis of variance. Value represents Wilk's Lambda test statistic.

Species	Variable	df	Value	F	Pr > F
Water Sedge	Nitrogen	3	0.03	89.31	0.0001
Water Sedge	Phosphorous	3	0.008	358.55	0.0001
Water Sedge	Digestibility	3	0.02	122.90	0.0001
Planeleaf Willow	Nitrogen	3	0.02	138.81	0.0001
Planeleaf Willow	Phosphorous	3	0.006	453.33	0.0001
Planeleaf Willow	Digestibility	3	0.04	57.47	0.0001

Appendix Table 2. Time by treatment interactions for N and P concentrations and digestibility (IVDMD) of water sedge and planeleaf willow current year's growth. Tests of the hypotheses that time by treatment interaction did not affect each variable were conducted using a repeated measures analysis of variance. Value represents Wilk's Lambda test statistic.

Species	Variable	df	Value	F	Pr > F
Water Sedge	Nitrogen	12	0.20	1.52	0.19
Water Sedge	Phosphorous	12	0.25	1.22	0.33
Water Sedge	Digestibility	12	0.23	1.32	0.28
Planeleaf Willow	Nitrogen	12	0.51	0.52	0.88
Planeleaf Willow	Phosphorous	12	0.18	1.61	0.16
Planeleaf Willow	Digestibility	12	0.13	7.53	0.0001

Appendix Table 3. Analysis of variance for the influence of treatment at each collection time on current year's growth of water sedge and planeleaf willow N and P concentrations and digestibility (IVDMD). All treatments, including controls, at all collection times are compared with one another. Tests of the hypotheses that treatment did not affect each variable at each collection time were conducted using a repeated measures analysis of variance.

Variable	Collection Time	df	Mean Square	F	Pr > F
Water Sedge					
Nitrogen	June 1	4	0.07	1.04	0.43
	July 1	4	0.04	1.63	0.24
	August 1	4	0.43	2.67	0.95
	September 1	4	0.02	1.16	0.39
Phosphorous	June 1	4	76.82	1.94	0.18
	July 1	4	24.82	0.82	0.54
	August 1	4	55.24	2.85	0.08
	September 1	4	16.31	0.90	0.50
Digestibility	June 1	4	10.71	1.17	0.38
	July 1	4	17.80	2.05	0.16
	August 1	4	6.25	1.82	0.20
	September 1	4	12.54	6.06	0.01
Planeleaf Willow					
Nitrogen	June 1	4	0.01	0.33	0.85
	July 1	4	0.03	0.74	0.60
	August 1	4	0.08	2.18	0.14
	September 1	4	0.07	1.16	0.06
Phosphorous	June 1	4	118.92	1.04	0.43
	July 1	4	150.80	0.84	0.53
	August 1	4	513.69	16.06	0.0002
	September 1	4	5.27	0.02	0.99
Digestibility	June 1	4	75.14	15.78	0.0003
	July 1	4	56.38	0.64	0.65
	August 1	4	25.18	10.32	0.001
	September 1	4	70.21	4.60	0.02

Appendix Table 4. Analysis of variance for the influence of grazing on N and P concentrations and digestibility (IVDMD) of current year's growth of water sedge and planeleaf willow. Tests of the hypotheses that grazing did not affect each variable were conducted using a univariate linear contrast statement.

Species	df	Nitrogen (%)			Phosphorous (%)			Digestibility (%)		
		Mean Square	F Value	Pr > F	Mean Square	F Value	Pr > F	Mean Square	F Value	Pr > F
Water Sedge	1	.19	3.21	0.10	.008	6.14	0.03	76.55	17.97	0.0017
Planeleaf Willow	1	.018	0.31	0.59	.015	1.51	0.25	66.27	3.26	0.1013

Appendix Table 5. Analysis of variance for the influence of species on N and P concentrations and digestibility (IVDMD) for current year's growth of water sedge and planeleaf willow. Tests for the hypotheses that species did not affect each variable were conducted using analysis of variance with 4 collection times. Treatments include grazed or browsed plants and controls.

			Pr > F		
Variable	**Species**	**Time**	**Treatment X Species**	**Treatment X Time**	**Treatment X Species X Time**
Nitrogen	0.0001	0.0001	0.06	0.33	0.79
Phosphorous	0.0001	0.0001	0.36	0.16	0.0001
Digestibility	0.0001	0.0001	0.33	0.23	0.0001

Appendix Table 6. Analysis of variance for total herbaceous standing crop, 1996.

General Linear Models Procedure
Class Level Information

Class	Levels	Values
TREAT	5	1 2 3 4 5
REP	3	1 2 3

Number of observations in data set = 150

Dependent Variable: WT

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	6	21900.0525	3650.0087	5.25	0.0001
Error	143	99400.5518	695.1088		
Corrected Total	149	121300.6043			

R-Square	C.V.	Root MSE	WT Mean
0.180544	39.50305	26.3649	66.7415

Source	DF	Type I SS	Mean Square	F Value	Pr > F
TREAT	4	8828.9822	2207.2456	3.18	0.0156
REP	2	13071.0702	6535.5351	9.40	0.0001

Source	DF	Type III SS	Mean Square	F Value	Pr > F
TREAT	4	8828.9822	2207.2456	3.18	0.0156
REP	2	13071.0702	6535.5351	9.40	0.0001

Appendix Table 7. Mean separation for total standing crop, 1996. Treatment 1 = Spring, 2 = Early-summer, 3 = Late-Summer, 4 = Fall, 5 = Control.

```
              T tests (LSD) for variable: WT

  NOTE: This test controls the type I comparisonwise error rate not
        the experimentwise error rate.

             Alpha= 0.05  df= 143  MSE= 695.1088
                  Critical Value of T= 1.98
            Least Significant Difference= 13.456

  Means with the same letter are not significantly different.

        T Grouping              Mean       N  TREAT

                 A            80.271      30  4
                 A
            B    A            68.557      30  5
            B
            B                 66.060      30  1
            B
            B                 59.410      30  2
            B
            B                 59.410      30  3
```